# MACROZAMIA MOOREI, A CONNECTING LINK BETWEEN LIVING AND FOSSIL CYCADS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 168

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(WITH TWELVE FIGURES)

The greatest cycad centers of the world are the states of Vera Cruz and Oaxaca in Mexico and Queensland in Australia, Queensland having three genera, *Cycas*, *Macrozamia*, and *Bowenia*, and the Mexican region three genera, *Dioon*, *Ceratozamia*, and *Zamia*. As yet no other region has claimed more than two genera. In the cycad region of Australia *Macrozamia* is the dominant genus, and its various species range from the northern part of Queensland to the southern limit of cycads in New South Wales. In a more extended publication the genus and the interrelationship of its species will be discussed, but at present we shall consider only a single species, *Macrozamia Moorei*, which presents features of unusual interest. The field study was made at Springsure, about 200 miles west of Rockhampton and almost on the Tropic of Capricorn.

*Macrozamia Moorei* has a massive cylindrical trunk with a splendid crown of leaves (fig. 1). Most of the plants grow in the blazing sun, but some are found in the scanty shade of small *Eucalyptus* and other trees. The altitude of Springsure is about 325 m., but some plants were noticed a few miles east of Springsure, perhaps 30 m. lower, and specimens could be seen on the tops of the neighboring mountains, perhaps 300 m. higher.

The trunk is 2–3 m. high in most of the large plants; a few reached 5 m. in height, and one specimen, growing in the shade, measured 7 m. from the ground to the bud. The diameter of the trunk of this specimen was 66 cm., but there is little increase in diameter after a plant reaches a meter in height, for such plants may be 0.5 m. in diameter, and some plants 3 m. in height, and growing in the sun, measured 71 cm. in diameter.

The foliage display is not surpassed by any cycad. The leaves are 2–3 m. in length and may number more than 100 in a single crown. With so many large leaves in a crown, and, in all probability, a new crown nearly every year, the trunk grows rapidly. Mr. J. W. KEIT, of Durban, South Africa, showed me an ovulate plant raised from a seed planted 30 years before, which had a stem reaching 25 cm. above the surface and bearing a fine crown of leaves and two large cones. Another plant, also raised from a seed

FIG. 1.—*M. Moorei* at Springsure: ovulate plant in foreground has trunk about 3.5 m. in height.

planted a few years before the one just mentioned, had a stem 40 cm. in height and had borne ovulate cones for several years. This shows that the plant grows very rapidly and produces cones at an early age. Although it is very probable that small cycads, like *Zamia*, produce cones at a still earlier age, this is the first instance, so far as I know, in which the period between the planting of the seed and the production of cones is known, even approximately.

The armor of leaf bases persists even at the base of the stem, so that the age of a plant could be estimated quite easily, if it were

known how often new crowns are produced. If crowns are produced every year, a plant a meter in height might be considerably less than 100 years old.

Although the trunk is so massive, a transverse section shows the large pith, scanty wood, and large cortex, so characteristic of cycad stems, there being no extensive development of wood like that found in large stems of *Dioon spinulosum*. A plant about 3 m.

FIG. 2.—*M. Moorei:* transverse section of stem 45 cm. in diameter

in height, with a stem 45 cm. in diameter, had a zone of xylem and phloem only 5 cm. in width (fig. 2). In the photograph three distinct regions are shown; the innermost is the xylem, the middle one its accompanying phloem, and the outermost a second cylinder with its xylem and phloem which show clearly in the material but which are not differentiated in the photograph. The trunk, therefore, is polyxylic. The outer cylinder evidently originates in the cortex, as in *Cycas*, but is separated from the primary cylinder by only a scanty amount of parenchyma. There are

scattered bundles in the pith, but there are no cone domes, and the scattered bundles seem to have no connection with cones. In regard to the bundles in the pith, this stem is somewhat like that of *Macrozamia Fraseri*, as described by WORSDELL.[1]

The tracheids of the xylem show two, three, or four rows of crowded bordered pits. There are uniseriate rays, similar rays two or three cells wide, and large rays containing vascular strands,

FIG. 3.—*M. Moorei:* ovulate cones about 76 cm. in length

as in *Dioon*. There is no more difference between the general and histological structure of the stems of *Macrozamia* and *Cycadeoidea* than may be found between different genera of Cycadales. Bennettitales and Cycadales could hardly be separated on the basis of stem structure.

The ovulate cones are large and are seldom borne singly, two, three, or four being more common than a single cone, and in one case

[1] WORSDELL, W. C., Anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. Ann. Botany 10: 601–620. *pls.* 27–28. 1896.

I saw eight large cones on a single plant (fig. 3). When I visited Springsure, late in November, the cones were not mature, but some of them were already 80 cm. in length and weighed 15 kilos. Dr. F. M. BAILEY, in his *Flora of Queensland*, reports cones 90 cm. in length. Scarcely any of the cones were vertical, nearly all leaning and some of them almost horizontal (fig. 1). The numerous strong leaves prevent the cone from hanging down, as it does in *Dioon spinulosum*.

FIG. 4.—*M. Moorei* with more than 50 staminate cones

By far the most striking feature of *Macrozamia Moorei* is its staminate cones and associated structures (fig. 4). Plants with 20–40 staminate cones were not at all rare, and in one case I counted 103 cones on a single unbranched plant. Not only is the number larger than has ever been reported for any cycad, but the cones are obviously lateral, as may be seen by a glance at the figure, which shows a girdle of cones outside the new crown and scattered among the leaves of the previous crown. Young cones of the next season are found among the bases of the leaves of the new crown, but there are no cones in the center of the crown.

A tangential section through the armor at the top of the stem (fig. 5) shows a condition exactly like that seen in WIELAND'S figures of *Cycadeoidea*. The peduncles of the cones, with their accompanying scale leaves, are wedged in among the leaf bases, and sections show that the cones arise in the axils of the leaves. Of course, the terminal peduncles of *Dioon* and similar forms finally become wedged in among the leaf bases, but the condition is secondary and is due to the sympodial nature of the stem; in

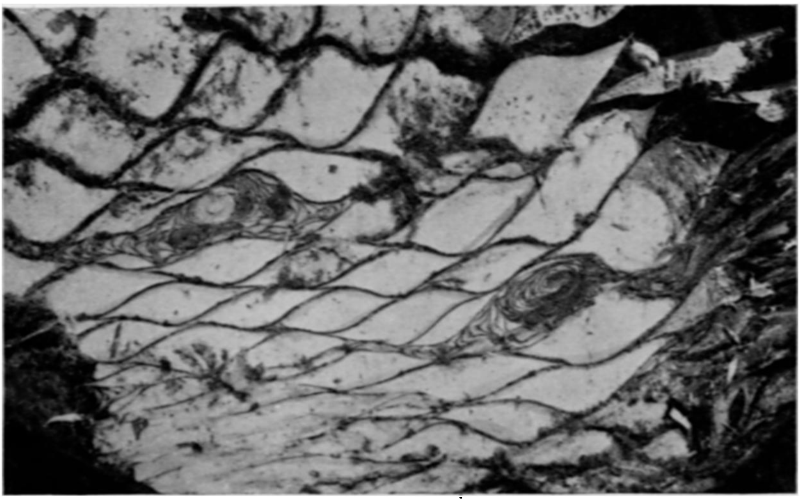


FIG. 5.—*M. Moorei:* tangential section (cut with an ax) through the armor of leaf bases, showing the peduncles of cones surrounded by scale leaves.

*Macrozamia Moorei* the condition is primary, the stem being monopodial, with all its cones lateral.

In all the occidental cycads, *Dioon*, *Ceratozamia*, *Microcycas*, and *Zamia*, a single ovulate cone is a rule to which there are scarcely ever any exceptions, except in *Zamia;* in staminate plants exceptions are almost as rare, except in *Zamia*, which very frequently has more than one cone, and sometimes as many as six or seven. In *Dioon*, *Ceratozamia*, and *Zamia*, in both ovulate and staminate plants, the cone domes in the pith indicate the sympodial nature of the stem. *Microcycas* has not been examined, but will doubtless show cone domes.

Among the oriental cycads (*Cycas*, *Macrozamia*, *Bowenia*, *Encephalartos*, and *Stangeria*) the situation is not so uniform. In *Cycas* the ovulate plant does not bear a compact cone, the sporophylls having the position of a crown of vegetative leaves with the growing point at the center, the growing point persisting from the seedling throughout the life of the plant. In the staminate plant there is hardly ever more than one cone, and this is terminal. There are cone domes in the pith.

In *Bowenia*, both ovulate and staminate cones are borne singly on slender branches of the main stem.

In *Stangeria*, both ovulate and staminate cones are terminal and are usually borne singly, although occasionally there may be two or three, especially in case of staminate plants. There are well marked cone domes in the pith.

In *Encephalartos*, both male and female plants often bear more than one cone, and in some species a single cone is the exception, while three, four, and five are common. PEARSON noted that in *Encephalartos Frederici Gulielmi* the cones are arranged in a circle about the bud. In this species, at Queenstown, South Africa, where PEARSON made his observation, I saw seven ovulate cones in a circle about a well developed bud. In *E. caffer*, *E. Altensteinii*, *E. horridus*, and *E. villosus* I found three to five cones in a circle about a well developed bud. Such cones are lateral with respect to the growing point, which does not become transformed into a cone, but continues the growth of the plant. A dissection of adult specimens of *E. Altensteinii* and *E. villosus* showed no cone domes in the pith, and cone domes are necessarily present when cones are terminal. It may be doubtful whether cones are terminal in *Encephalartos*, even when produced singly.

In various species of *Macrozamia* ovulate plants frequently bear more than one cone, and in staminate plants more than one cone is the rule. Both ovulate and staminate cones are obviously lateral, even when borne singly. There are no cone domes in the pith.

Of course, in all the genera, when there is branching in the popular sense of the term, each branch may bear a cone.

Since *Macrozamia Moorei* approaches so closely to the Ben-

nettitales, it is worth while to consider how a compact cone has probably been derived from a loose crown of sporophylls, and how the terminal position of cones may have succeeded the lateral. The compact cone, found everywhere in living cycads, except in the ovulate plant of *Cycas*, has in all probability been derived from a loose crown of sporophylls like those of the Cycadofilicales and the staminate sporophylls of Bennettitales, and like the ovulate sporophylls of *Cycas*. Various species of *Cycas* show stages in the advance from this loose crown of leaflike sporophylls toward the compact cone composed of sporophylls so highly modified that their leafy nature is very much obscured. In *Cycas revoluta* the sporophylls are quite leaflike and bear five or more ovules; in *C. circinalis* the pinnae are much more reduced, appearing only as serrations on the edge of the much reduced blade; in *C. media* the sporophyll is equally reduced and frequently bears only two ovules; in *C. Normanbyana* the sporophyll is about as in *C. media*, but there are regularly only two ovules. From the sporophyll of *C. Normanbyana* to that of *Dioon edule* the transition is easy, and the loose cone of *D. edule* does not differ much in appearance from early stages in the development of the ovulate structures of *Cycas*. The distinguishing feature is that in the ovulate plant of *Cycas* the meristem never becomes converted into sporophylls, but continues the growth of the axis. From the condition in *Dioon* to the more compact cones of the remaining genera, the transition is easier still, and consists principally in shortening the blade of the leaf until it finally reaches the almost peltate sporophyll of *Microcycas* and *Zamia*. Occasionally a proliferating cone reminds one of the *Cycas* condition.

In the reduction of the number of cones, and in the evolution of the compact cone from a loose crown of sporophylls, we have two independent series of changes, which may or may not have progressed with equal rapidity. Loose staminate sporophylls and numerous lateral cones are characteristic of the Bennettitales. The combination of loose sporophylls and numerous lateral cones is not found in any living cycad, but loose sporophylls are found in the ovulate plant of *Cycas*, and numerous lateral cones are found in *Macrozamia Moorei*, the staminate cones being almost as numerous

as in Bennettitales; while in other species of *Macrozamia* and in *Encephalartos* the lateral cones are present but not so numerous. In a reduction from numerous lateral cones to a single cone, the natural limit would be the single terminal cone developed from the apical meristem, and with the transformation of the apical meristem into a cone, the formation of a cone dome in the pith would be a necessary consequence. Accordingly, the absence of cone domes from *Macrozamia* and *Encephalartos* is easily understood.

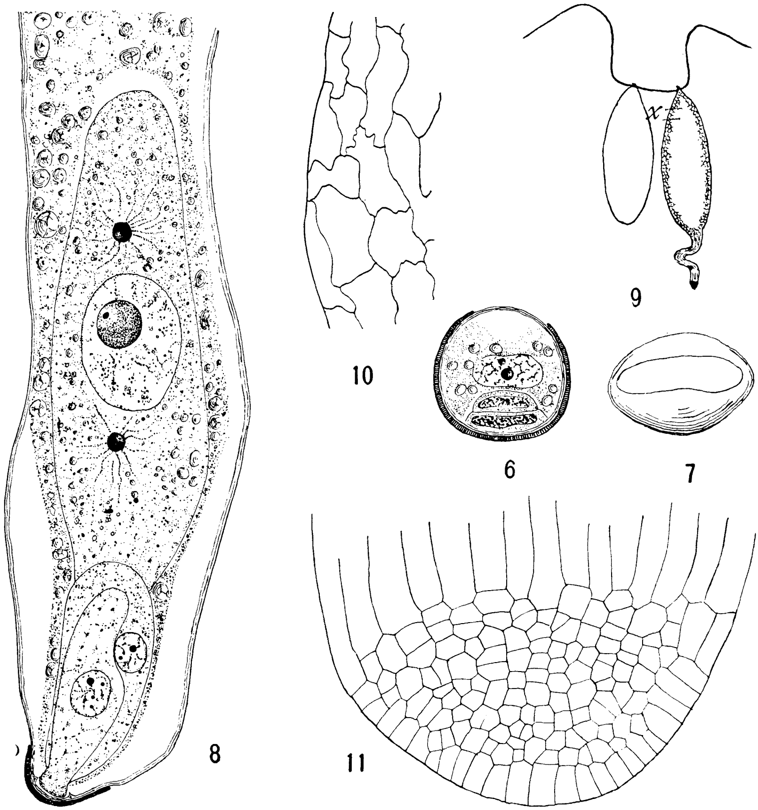
*Macrozamia Moorei*, in its numerous lateral cones and in their mode of occurrence, presents a condition identical with that found in *Cycadeoidea* among the Bennettitales. As far as the mode of bearing cones is concerned, *Macrozamia Moorei* makes the transition from Bennettitales, like *Cycadeoidea*, to the modern cycads an easy one. In the structure of the individual cone, the transition is not so easy, but may become less difficult when more is known about the cones of the Bennettitales, especially the lower Bennettitales. The connection between the higher Bennettitales and the Cycadales, already a close one, is made still closer by *M. Moorei*, so that it might be doubted whether the differences are great enough to distinguish orders.

## The male gametophyte

The pollen grain at the time of shedding contains three cells, a persistent prothallial cell, a generative cell, and a tube cell (fig. 6). As pollen shaken out from the cone loses a little moisture, it begins to collapse so that in a vertical view the grains appear elliptical, with a long narrow area at the top which does not stain when safranin is added (fig. 7). This elongated area becomes narrower as the grain dries and finally the sides come into contact. A study of sections shows that this elongated area at the top of the grain is not covered by the exine, but only by the intine, a situation which is constant in *Ginkgo*, but which has not been noted in cycads. Just beneath the portion not covered by exine there is usually a funnel-shaped depression. The cytoplasm of the pollen grain is quite dense and contains starch.

The pollen from which figs. 6 and 7 were drawn was shaken from a cone in the Botanic Gardens at Sydney on November 3, 1911,

and the condition of the staminate cones in the field at Springsure, about 1100 miles farther north, on December 1 would indicate that in the field the pollen had been shed at about the same time, or perhaps a little earlier. On December 1 the generative cell has




FIGS. 6–11.—*M. Moorei:* fig. 6, pollen grain at the shedding stage, November 3, 1911, showing prothallial cell, generative cell, tube cell, and starch grains; ×800; fig. 7, pollen grain; the elongated area is not covered by exine; ×800; fig. 8, pollen tube, December 1, 1911; ×480; fig. 9, upper part of female gametophyte, February 1912, showing deep archegonial chamber and young embryo; ×6; fig. 10, portion of parietal tissue of proembryo at *x* of fig. 9; ×130; fig. 11, tip of embryo shown in fig. 9; ×58.

already divided, forming the stalk and body cells, and the blepharoplasts have appeared (fig. 8). The pollen tube structures at this stage are about as in *Dioon*, there being scarcely any branching of

the tube and none of the peculiar basal haustoria which characterize the pollen tubes of *Ceratozamia*.

The condition of the male gametophyte when the pollen is shed is remarkably uniform in the family, no exception to the three-celled stage having as yet been demonstrated. IKENO found this condition in *Cycas revoluta*, and Miss FRANCES G. SMITH found it in *Encephalartos villosus*. I have observed it in *Dioon edule*, *Ceratozamia mexicana*, *Microcycas calocoma*, *Zamia floridana*, *Bowenia spectabilis*, *Macrozamia Miquelii*, *M. spiralis*, and *Stangeria paradoxa;* so that it occurs in all the genera. The behavior of the three cells is also similar, the prothallial cell pushing up into the stalk cell in all the genera, with the possible exception of *Cycas*.

Since the structure of the pollen grain is so uniform in the cycads, it would be interesting to know just what the structure is in fossil Cycadales and Bennettitales. A more extensive development of prothallial tissue and a comparatively slight development of the pollen tube or haustoria might be anticipated.

## The female gametophyte

Early in November, when the ovulate cones have attained a length of 78 cm., the female gametophyte has reached its full size, but by no means its full density. The archegonia, generally 4–6 in number, are a little more than 3 mm. in length and are becoming filled with protoplasm and foodstuffs. The ventral canal nucleus has not yet been cut off and the archegonial chamber has just begun to develop. At the fertilization stage, most of the cells of the female gametophyte contain large starch grains; the rest contain tannin. The archegonial chamber is the deepest ever noted in a cycad, the average depth being about 1.8 mm., so that the depth is nearly two-thirds as great as the length of the archegonium (fig. 9).

## The embryo

The earlier stages in the development of the embryo are not available, but arrangements have been made to secure them. The earliest stage in our material is shown in fig. 9. At this stage *Macrozamia Moorei* differs from *Dioon edule*, *Ceratozamia mexicana*, and *Zamia floridana*, but agrees with *Cycas revoluta* and perhaps

with *C. circinalis*. In *Zamia* and *Ceratozamia* fertilization is followed by a series of free nuclear divisions and finally cell formation takes place only at the bottom of the egg, less than one-fifth of the egg becoming segmented, while the rest remains in the free nuclear condition. In *Dioon edule* the free nuclear stage is followed by an evanescent segmentation of the entire egg, but later

FIG. 12.—*M. Moorei:* a poisoned plant

stages show segmentation only at the bottom of the egg, with free nuclei above. *Macrozamia Moorei*, in the only stages available, shows complete segmentation, but a large vacuole has already developed, and within the limits of the egg there remains only a cellular layer two or three cells in thickness (fig. 10). Material of *Cycas revoluta* in this stage, furnished me by IKENO several years ago, shows exactly this condition. Whether both have passed through a stage of complete segmentation, as in *Ginkgo*, or segmentation

has occurred only at the periphery, the vacuole having been formed by the breaking down of free nuclear material, are questions which could be answered by a glance at material in the desired stages. The extensively segmented proembryos of *Macrozamia* and *Cycas*, and even the temporarily segmented proembryo of *Dioon*, are, in our opinion, more primitive than the proembryos of *Zamia* and *Ceratozamia*, which are segmented only at the base.

At the stage shown diagrammatically in fig. 9 and quite accurately in fig. 11, the differentiation into suspensor and embryo proper is quite distinct, but there is not yet any differentiation of plerome and periblem or even dermatogen; the outer layer of large absorbing cells still showing numerous periclinal divisions.

Unfortunately, the young leaves of *Macrozamia* contain a poison which causes a kind of paralysis in cattle, and consequently the plant is in bad repute among cattlemen. At Springsure, the only habitat mentioned for *M. Moorei*, the plant is being exterminated so rapidly that in a few years it may be hard to find a specimen. In killing the plant, a notch is chopped in the trunk and a large hole is then bored from the notch to the center of the pith (fig. 12). The hole is filled with arsenic and the plant soon dies. The dead specimens become quite brittle and are soon broken down by the wind. The notch and the characteristic appearance of a poisoned specimen are shown in fig. 12. The species is beautiful and grows rapidly, but it is almost never found in botanical gardens and conservatories. It would be a pity to allow a plant with such good claims to the title of missing link to become extinct, in spite of the fact that it is easily accessible.

## Summary

1. *Macrozamia Moorei* bears numerous lateral cones in the axils of leaves, in this respect being identical with the mesozoic Bennettitales.

2. The pollen grain, at the time of shedding, contains a persistent prothallial cell, a generative cell, and a tube cell; the exine does not cover the apical part of the grain. In the young pollen tube the generative cell has given rise to a stalk cell and a body cell like those of other cycads.

3. The archegonial chamber is unusually deep, and the archegonia are of moderate size.

4. The embryogeny resembles that of *Cycas* and differs from that of *Zamia* and *Ceratozamia*.

5. The species, which represents the nearest approach to the mesozoic Bennettitales, is in immediate danger of extinction.

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